Nest monitoring does not affect nesting success of Whinchats *Saxicola rubetra*

Jennifer A. Taylor[1], Ian G. Henderson[2], Ian R. Hartley[1]

[1]Lancaster Environment Centre, University of Lancaster, Lancaster, LA1 4YQ, UK. E-mail: j.taylor7@lancaster.ac.uk; i.hartley@lancaster.ac.uk

[2]British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK. E-mail: ian.henderson@bto.org

Abstract

It is important to assess the effect that research activities may have on animals in the wild, especially when key parameters, such as breeding success, could potentially be influenced by observer activity. For birds, some studies have suggested that nest monitoring can increase the chances of nest failure due to predation, while others suggest that human nest visits may actually deter mammalian predators. Nest monitoring visits can also influence breeding success more indirectly by altering parental provisioning behaviour. Here, the influence of monitoring activities on nest success in a ground nesting, grassland bird, was examined. First, during the egg phase, a sample of nests were not visited between the initial finding event and the estimated hatching date; instead the nest status was assessed from afar. Daily Survival Rates (DSR) for these nests were compared to nests visited every two days. Second, during the nestling phase, the effects of observer nest visits on parental provisioning behaviour were determined. Nest visits were found not to significantly affect egg DSR and parental provisioning was disrupted for a maximum of 20 minutes (0.52% of the nestling period) following an observer visit. Therefore we conclude observer visits have minimal effects on nest success in Whinchats.

Introduction

Accurate quantification of breeding success in birds almost always requires nest visits by the researcher. There has long been concern that these necessary visits may impact a bird's breeding success, biasing estimates and possibly reducing breeding success in the very species scientists are aiming to conserve or understand (Reynolds & Schoech 2012). Reviews on the topic have found that effects of researcher visits to nests vary widely among species, sometimes even within the same habitat (Weidinger 2008; Ibanez-Alamo *et al.* 2012). It is, therefore, particularly important for researchers to monitor the effect of disturbance from their research activities and use this information

when interpreting their findings and when planning future research projects (O'Grady *et al.* 1996; Price 2008; Reynolds & Schoech 2012).

Disturbance by researchers during nest monitoring activities can potentially influence the outcome of a nest either directly, by encouraging nest desertion (Tremblay & Ellison 1979; Piatt *et al.* 1990), or indirectly, by increasing the risk of predation. Parents may be forced to leave nests unguarded (Strang 1980) and researchers may draw attention to a nest by creating olfactory or visual trails leading to it (Whelan *et al.* 1994) and eliciting conspicuous parental defence behaviours such as alarm calling (Major 1990; Weidinger 2008; Jacobson *et al.* 2011). A review by Götmark (1992) found researcher activities had reduced nesting success in 49% of studies but a recent meta-analysis on 25 species from six orders found that researcher visits did not affect the probability of nest failure through predation (Ibanez-Alamo *et al.* 2012). In fact, nest visits by observers may actually have reduced the risk of predation for passerines and ground nesting birds, as the presence of humans may deter mammalian predators (Macivor *et al.* 1990; Ibanez-Alamo & Soler 2010; Ibanez-Alamo *et al.* 2012, but see Skagen *et al.* 1999).

Nest monitoring visits also can affect breeding success by altering the parents' behaviour. Animals tend to respond to human disturbance as though it was a potential predation event (Frid & Dill 2002; Beale & Monaghan 2004; Price 2008). This may lead to a temporary suspension of nestling provisioning (Wheelwright & Dorsey 1991; Michl *et al.* 2000; Zhao 2005; studies reviewed in Lima 2009; Tilgar *et al.* 2011; Paclik *et al*. 2012; Ghalambor *et al.* 2013; Mutzel *et al.* 2013; Vitousek *et al*. 2014; but see Hakkarainen *et al.* 2002) and a corresponding increase in vigilance, nest guarding and nest defence behaviours (Montgomerie & Weatherhead 1988; Wheelwright & Dorsey 1991; reviewed in Frid & Dill 2002 and Price 2008; Caro 2005; Mutzel *et al*. 2013). This behaviour is potentially adaptive, as the risk of the predator finding the nest is reduced (Eggers *et al*. 2005, 2008), the parent can invest more time and energy in active nest defence (Montgomerie & Weatherhead 1988) and the parents' survival chances may also be increased (Lima 2009). There is, however, a trade-off in that the food supply to the nestlings is reduced, which can impact offspring condition and possibly their future survival chances and reproductive output (Trivers 1972; Clark & Ydenberg 1990; Dale *et al.* 1996; Michl *et al.* 2000; Frid & Dill 2002; Price 2008; Martin & Briskie 2009; Lima 2009). When disturbance is repeated and frequent, the temporary suspension of feeding has the potential to cause harmful cumulative consequences, with young fledging at smaller sizes (Scheuerlein & Gwinner 2006; Thomson *et al.* 2006; Tilgar *et al.* 2011). Some studies found that parents will compensate by provisioning at a higher rate after a predation threat (Paclik *et al.* 2012; Mutzel *et al.* 2013 but see Tilgar *et al.* 2011) and by provisioning larger load sizes (Eggers *et al.* 2008; Lima 2009). However,

there is limited scope for compensation as a nestling's digestive system can only process a certain quantity of food within a given time period (Eggers *et al.* 2005).

The response of the parents to a perceived 'predation threat' will vary depending on the balance between the potential 'value' of the nestlings and on the perceived risk to the parents (Trivers 1972; Montgomerie & Weatherhead 1988; Clark & Ydenberg 1990). The potential 'value' of the nestlings depends on nestling age (Dale *et al.* 1996; Michl *et al.* 2000; Pavel & Bures 2001; Zhao 2005), brood size (Tilgar & Kikas 2009), nestling condition (Michl *et al.* 2000), the parent's investment so far (Dale *et al*. 1996; Pavel & Bures 2001) and the potential for re-nesting (reviewed by Martin 1987; Michl *et al.* 2000). For example, parents may risk more and resume feeding earlier for larger broods (Tilgar & Kikas 2009) or nestlings in better condition (Michl *et al.* 2000) and female parents may take more risks than male parents for younger nestlings if they have invested more in the nestlings up to this stage (Michl *et al*. 2000; Pavel & Bures 2001; Dale *et al*. 1996). The perceived risk to each parent may depend on the type of predator (Bures & Pavel 2003; Martin & Briskie 2009; Tilgar *et al.* 2011; Ippi *et al.* 2013), the sex, size, condition and experience of the parent (Martindale 1982; Montgomerie & Weatherhead 1988; Lima 2009), and the protection offered by the surrounding nesting habitat (Eggers *et al.* 2008; Lima *et al*. 2009; Martin & Briskie 2009). For situations where a species can actively defend the nest against a predator, parents may remain close to the nest following a predation threat, and restrict their foraging range (Marzluff 1985; Martindale 1982; Hakkarainen *et al.* 2002; reviewed in Lima 2009). The parent that is most effective at defending the nest often remains closer to the nest than their partner (e.g. Gila Woodpecker, Martindale 1982). In species where neither parent is actively able to defend the nest contents against predators, the optimal strategy is likely to be nest crypsis and the minimisation of parental activity around the nest (Burhans 2000; Bures & Pavel 2003).

In this paper we aim to explore the potential effects of visiting Whinchat nests to monitor reproductive success. Daily survival rates during the egg phase will be compared between nests which received visits every two days, and those that were visited only once. Previous studies suggest that where the main predators are mammalian, as appears to be the case in this study (Taylor *et al.* in prep), the nest predation rates may be reduced by more frequent monitoring visits. Additionally, we quantify the provisioning behaviour of parents in relation to researcher nest visits. It is predicted that the Whinchat parents will reduce nestling provisioning until the perceived threat has diminished to avoid disclosing the nest location and to allow more time to be allocated to nest guarding and vigilance behaviours. To this end, it is also predicted that parents are likely to remain in the vicinity of the nest immediately after a predation threat, to enable earlier nest predator detection, and will avoid long foraging trips until the perceived threat has diminished.

Methods

Study site

The study site was located on the west section of Salisbury Plain, Wiltshire, in southwest England (51°11'52" - 51°16'4"N; 1°57'32" - 2° 9'32"W). The site has been under military ownership since the early 20th century and the west section is predominantly used by the military for training. The majority of the area is classified as agriculturally unimproved grassland (Walker & Pywell 2000)..

Nest visit experiment during egg phase

Nests were found for all known breeding pairs within the study site. The locations of all nests were recorded using a Geographical Position System (GPS) reading at the nest site. Nests were also marked in the field using an unobtrusive 50cm bamboo cane 2-3 m from the nest. In 2014, nests were paired in the order of finding, with alternate nests being designated as 'visit' nests and 'distance-visit' nests. Daily watches of breeding adults early in the season and recording of behaviour and nest building activity enabled hatching date to be estimated to within two days. Visit nests were visited every two days and distance-visit nests were not visited after the initial nest finding event, until the estimated hatching date. Distance-visit nests were assessed from a distance every two days, to determine whether they were still active, by observing the female leaving the nest and returning to incubate, or via alarm calling parents on the territory when the researcher was in the vicinity. After the initial nest finding, the observer never went closer than 20 m to the distance-visit nests and, in general, stayed at least 80 m away.

Disturbance experiment during nestling provisioning

Thirty-nine monitored nests were included in the experiment: 20 in 2013 and 19 in 2014. The researcher approached the nest and set up a small video camera on a tripod, pointing at the nest, one metre away. Marker canes were placed into the ground at 20, 40, 60 and 80 m from the nest, to facilitate distance estimation. The observer then retreated to at least 80 m to watch the parents during their subsequent provisioning activities. The video camera recorded provisioning visits by the parents, and the observer recorded the parents' distances from the nest once every minute for the hour following the disturbance event. To account for the variable nature of provisioning rates the experiment was conducted on each nest three times, when the nestlings were 6, 7 and 8 days old; the period of maximum provisioning rate. Provisioning watches were conducted between 9 am to 6 pm, which avoided times when feeding rates may be particularly high or when the need to feed nestlings would be more urgent. Watches were not conducted in moderate to heavy rain. Due to weather conditions, access restrictions and predation of nests, there were some cases where it was not possible to undertake all three replicates (25 nests with 3 days of data, 8 nests with 2 days of data and 4 nests with 1 day of data). Provisioning data from two nests were excluded: one because of technical

problems with the camera and one because the local topography prevented observations without disturbing the birds.

Nestling condition

Six days after hatching, all nestlings were weighed and had their tarsi measured, although due to occasional access restrictions, this occurred a day either side in a minority of cases. An index of body condition was calculated by regressing an individual's weight (g) against their size (measured by tarsus (mm)) and by extracting the residuals for use in the analysis (Davies *et al.* 2014). Body condition was normally distributed. The necessary assumptions that mass and tarsus length were linearly related (LM: Est = 0.813 +/- 0.021, $p < 0.0001$, $n = 385$) and that condition was independent of tarsus length (Pearson's Product Moment Correlation Coefficient (PMCC) = -1.56, df = 385, $p = 1$) were upheld (Green 2001). Nestling body condition was then averaged for nestlings within a nest to produce a mean value per nest.

Data analysis

The data were analysed using the R statistical package version 2.3.1 (R Development Core Team 2014). A logistic exposure model (see Shaffer 2004), with 'visit' or 'distance-visit' as a factor, was used to assess the influence of nest visits on the Daily Survival Rate (DSR) for the egg phase of the breeding cycle. Only first broods were included in the analysis to avoid pseudo-replication. The time since the disturbance event was split into 12 five-minute periods, with the number of feeds calculated for each observation period and then averaged over the three replicates for each nest. Based on pilot data from 2012, five minutes was selected as long enough to allow provisioning events to occur, but short enough to detect the gradual pattern of change in provisioning rate after a predation event. The sex of the provisioning parent was determined in 98% of feeds. The number of feeds per five-minute period was positively skewed and therefore was square root transformed for use in the analysis. A Non-linear Least Squares (NLS) model of the form: asymptote/(1 + exp((midpoint – time since nest disturbance)/slope)), was used to produce an equation for the relationship between time since disturbance and parental provisioning rate to determine the length of time provisioning was disrupted. GAMMs were used to examine the variation in number of feeds with parental sex, brood size and nestling condition.

Linear Mixed Models (LMM) were used to assess the time until the first feed after nest disturbance (latency to feed), and how this varied due to parental sex, brood size and chick condition, with nest as the random effect. The latency to feed was positively skewed and therefore was square root transformed to an approximately normal distribution. The global model, which included two interaction effects of parental sex and brood size and parental sex and nestling condition, was

simplified via backwards stepwise deletion using the drop1 command in R (Chambers 1992). For each nest, the mean latency to feed for both parents was calculated over the 1 – 3 observation periods.

The percentage of time spent 20 m or less from the nest was investigated in the same way as the number of feeds: the data were split into 12 five-minute blocks of time. For each block the number of distance observations where a parent was 20 m or less from the nest was divided by the total number of distance observations for that parent within the five minute block. This percentage was then averaged for each 5 minute block over the 1-3 observation periods per nest. The percentage of time spent 20 m or less from the nests was selected because within 20 m was considered a distance that the parents could still see the nest, and any approaching predator from, well before the predator got close enough to attack, therefore suggesting a preference for nest guarding and vigilance. The percentage of time spent 20 m for less from the nest was positively skewed, however, transformation did not improve the distribution, and the final model residuals did not reflect any problems despite the skew.

Results

Effect of nest visits on egg survival

There was no significant difference in the Daily Survival Rate for the egg phase between visit and distance-visit nests (Logistic-exposure GLM: ANOVA, $p = 0.569$, $df = 122$, $n = 124$ observation intervals from 17 visit nests and 18 distance-visit nests).

Effect of nest visits on parental provisioning behaviour

The starting values for the NLS model were chosen based on Figure 1. To account for the repeated measures of the 12 five minute blocks for each nest, a global model with a random effect of nest was used (AIC = 618); this had a lower AIC than the global model with nest and year random effects (AIC = 620) and the global model without a random effect (AIC = 695). The model parameters are displayed in Table 1. Residual plots confirmed the model was a good fit. After a nest disturbance event, the parental provisioning rate increased up to a maximum level at around 20 minutes where it levelled off (S1). This asymptote translates to 1.12 feeds (95% CI: 1.11 – 1.14) in five minutes.

Variations in parental response to disturbance due to parental sex and nestling condition

The global model allowed different smoothing slopes for the provisioning rates for each parental sex and included a parental sex and condition interaction and a brood size term. A model allowing the smoothing slope to change with nestling condition was too complex to fit with the data available: separately evaluating this model without the other variables indicated that there was not a significant change in slope with condition. A global model with a random effect of nest had an AIC of 1042, as opposed to a global model with year and nest as random effects, AIC = 1044, and a global model

without random effects, AIC = 1190. Therefore only a random effect of nest was used. The best model had a smoothed term for time since disturbance, and included parental sex and brood size terms (Table 2). Brood size did not have a significant effect on the provisioning rate (GAMM: $p > 0.223$) but it was included in all models as a control for variations in brood sizes between nests.

There was a marginally significant difference in the response of males and females, with males provisioning generally at a higher rate: (GAMM: Est = 0.0709 +/- 0.0292, p = 0.0152, n = 852 observations from 37 groups, Figure 1) but, as GAMMs rely on approximation, only probabilities less than 0.01 provide strong evidence of an effect (Zuur *et al*. 2009). The smoothed term is highly significant ($p < 1 \times 10^{-16}$), and the model AIC without the smoothed term is much higher (Table 2), indicating the smoothed term is necessary. Residual plots confirmed the global model and end model were both good fits for the data.

Latency to feed

The global model had a brood size and parental sex interaction and a nestling condition and parental sex interaction. A random effect of nest did not change the AIC value (both equalled 236), but a linear mixed model was used anyway to give a conservative model. None of the variables had a significant effect on latency to feed and all dropped out of the model in backwards stepwise deletion (Likelihood ratio test: $p > 0.177$).

Parental distance from the nest with time after a predation threat

Initially the pattern in the data was explored by via a GAMM. A GLMM (Generalised Linear Mixed Model) was considered suitable as the effective degrees of freedom (edf) from the GAMM was 1, which indicated that the data followed a linear trend. Ideally a binomial model should be used as the dependent variable is in the form of a proportion and therefore bounded between 0 and 1. However, a binomial model gave warning messages due to the lack of variability in the data. Therefore, a Gaussian model was also fitted to confirm the results. For both models, the end results were qualitatively similar, therefore only the results of the Gaussian GLMM are reported.

The AIC was lower for a global GLMM model just with nest as a random effect as opposed to territory and year (-132 as opposed to -130), both random effect models were better than a GLM without random effects (AIC = -9.74). The AIC reduced when the sex and time since disturbance interaction was removed (AIC = -145 as opposed to -131). The amount of time that the parents spent within 20 m of the nest did not change significantly with increasing time since the nest disturbance event (GLMM: Est = 0.000446 +/- 0.000408, df = 0.0844, t = 1.09, p = 0.275, n = 885 observations in 39 groups). Males spent significantly less time within 20 m of the nest than females (GLMM: Est = -0.0550 +/- 0.0143, df = 0.0855, t = -3.85, p = 0.000125, n = 885 observations in 39 groups). However,

231 the magnitude of the difference was small, with males spending about 5% less time within 20 m of the
232 nest than females. The variance of the random intercept for nest was 0.0149.

233 Discussion

234 Despite the study site consisting largely of unmanaged grassland, where researcher trails may be more
235 obvious compared to sites with shorter vegetation, monitoring visits to nests did not significantly
236 increase the chances of nest failure. This supports the findings from similar studies of ground-nesting
237 grassland birds (Cotter & Gratto 1995; O'Grady *et al.* 1996; Lloyd *et al.* 2000; Jacobson *et al.* 2011).
238 Salisbury Plain supports large populations of other species of ground nesting birds including Meadow
239 Pipits, Skylarks, Yellowhammers and Reed Buntings (Stanbury *et al.* 2002, 2005) and there were
240 many other trails in the vegetation from related work on Whinchats and from other people such as
241 soldiers training, farmers, security forces and other researchers. Therefore, the predators may not have
242 learned to associate trails with nests (Hannon *et al.* 1993; O'Grady *et al.* 1996; Weidinger 2008). The
243 main predators of nests on Salisbury Plain were found to be nocturnal (Taylor *et al.* in prep), which
244 suggests mammalian predators. Various other studies have found that mammalian predators are
245 deterred by human scent trails and therefore visited nests are actually less likely to be predated
246 (Macivor *et al.* 1990; Ibanez-Alamo & Soler 2010; Ibanez-Alamo *et al.* 2012). However, this pattern
247 was not observed in this study. The lack of organised predator control on Salisbury Plain, along with
248 the random nature of scent trails discussed above, could explain the lack of deterrence of mammals to
249 human scent trails. Alternatively, different predators may vary in their response to human scents, for
250 example with foxes deterred but stoats attracted, so thereby leading to no overall effect (Jacobson *et*
251 *al.* 2011).

252 Nest disturbance temporarily reduced the provisioning rate of parents; similar effects of disturbance
253 have been found in other studies (e.g. Delaney *et al.* 1999; Steidl & Anthony 2000; Verhulst *et al.*
254 2001). This parental response is considered an adaptation to: reduce the risk of revealing the nest
255 location, allow more time to be invested in defence and vigilance behaviours, and reduce adult
256 predation risk (reviewed in Martin & Briskie 2009 and Lima 2009). However, parental response to a
257 perceived predation risk can have real consequences on breeding success (Zanette *et al.* 2011).

258 It took approximately 20 minutes for the provisioning rate to recover, assuming the asymptote of the
259 NLS model (Table 1) represents the undisturbed provisioning rate. The mean provisioning rate
260 recorded for undisturbed nests of nestlings in approximately the same age range (5 – 8 days old), from
261 pilot data in 2012, was 1.35 feeds (95% CI: 0.983 – 1.73, n = 16 nests) in five minutes. The asymptote
262 provisioning rate of 1.12 is within this range, therefore supporting this assumption. In an average
263 summer day there are 960 minutes of daylight, therefore 2.08% of the day's provisioning is affected
264 by disturbance from a nest visit during the day. When not conducting the disturbance experiment,

nests were visited three times in the 12 – 13 days of the nestling period, which is 60 minutes of reduced provisioning out of 11520 minutes (0.52% of the nestling period). The Whinchat parents may have reacted more strongly to disturbance in this experiment due to the presence of the camera and tripod at their nest in addition to the researcher visit, therefore this disturbance estimate is conservative. It does not appear that disturbance, at the level usually undertaken by researchers during the nestling phase in this project, would adversely affect offspring fitness.

Unlike results reported elsewhere, the change in the provisioning rate after disturbance and the latency to return to feed did not vary significantly with parent sex (Dale *et al.* 1996; Michl *et al.* 2000; Pavel & Bures 2001; Zhao 2005), brood size (Tilgar & Kikas 2009) or nestling condition (Michl *et al.* 2000). It is possible that this was due to the age of the nestlings used in the experiment. In Whinchats, parental care is female biased, with only females incubating the eggs and brooding the nestlings, though both sexes provision the nestlings (Cramp 1988). Therefore, nestlings may have more reproductive value to the female early in life than the male. The pilot data from 2012 suggested that the males' proportional investment in the nestlings (reflected in his provisioning behaviour) increased as they aged. Therefore by 6 – 9 days old the nestlings are probably equally valuable to both parents (as also suggested by Tilgar & Kikas 2009). The lack of an effect of nestling condition and brood size on the provisioning rate and latency to feed may be due to a lack of variation in nestling condition on Salisbury Plain as food does not appear to be limiting at the site (Taylor *et al*. in prep). If this study was conducted on a site with larger variations in nestling condition, a difference in risk taking for different quality broods (Michl *et al.* 2000; Tilgar & Kikas 2009) may have been apparent.

The percentage of time the parents spent 20 m or closer to the nest did not vary significantly with time since the nest disturbance event. Parents generally always spent a high percentage of their time (70 – 80%) within 20 m of the nest. Preliminary analysis using the actual distances of parents from the nest, rather than the percentage of time parents spent within 20 m, also found no change in the mean distance over time. As food appears to be relatively abundant on the study site, the parents may not need to travel far from the nest to forage (Andersson 1981), allowing them to spend most of their time close to the nest and thereby be able to guard the nest more effectively (Marzluff 1985; Martindale 1982; Hakkarainen *et al.* 2002; reviewed in Lima 2009). Whinchats cannot aggressively defend their nests from approaching humans, or other predators, by attacking. However, they do use alarm calling and perching in close proximity to the approaching individual to quiet their young and as distraction techniques (Montgomerie & Weatherhead 1988; Caro 2005; Lima 2009). The change in provisioning pattern suggests Whinchats did spend a larger proportion of their time exhibiting nest guarding or vigilance behaviours immediately after a nest disturbance event, rather than foraging to provision nestlings, and then this reduced over time leading to an increased provisioning rate (reviewed in Frid & Dill 2002, Price 2008 and Lima 2009).

From this study we have found that nest monitoring visits every two to three days are not detrimental to Whinchat breeding success. Visits did not significantly affect the egg phase DSR and though parental provisioning rates were reduced for about 20 minutes following the disturbance, this equates to only 0.52% of the available foraging time during the nestling phase and therefore is unlikely to have a severe impact on nestling development. This is reassuring as it suggests that routine monitoring activities did not affect the outcome of nesting attempts. However, it is still important to take precautions to minimise any potential impact (Jacobson *et al.* 2011; Reynolds & Schoech 2012) and follow guidelines for nest monitoring (Martin & Geupel 1993; Ferguson-Lees *et al.* 2011). Depending on the research aims, it may be possible to use temperatures sensors placed in nest cups to monitor clutch and brood survival, reducing the number of visits necessary (Hartman & Oring 2006; Weidinger 2006; Jacobson *et al.* 2011; Mougeot *et al.* 2014), or to monitor using micro-nest cameras which has the added advantage of identifying the nest predators (Pietz & Granfors 2000).

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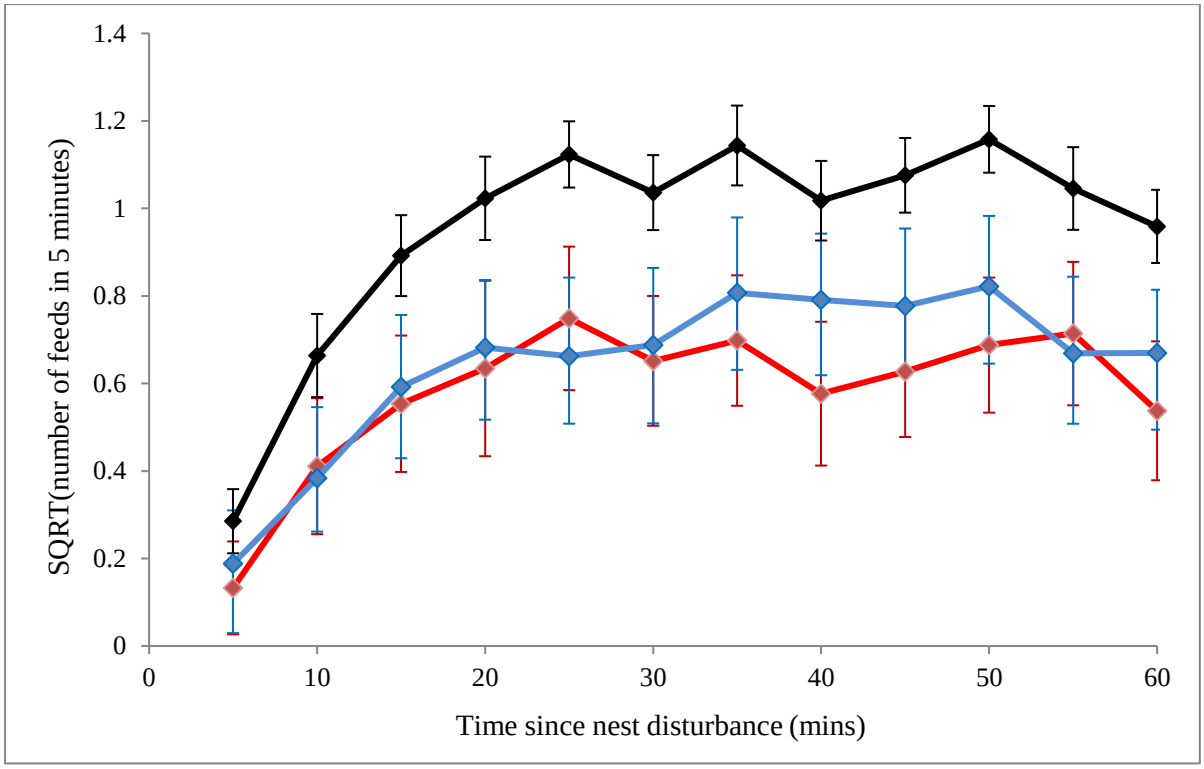


Figure 1. The square rooted mean number of feeds for all feeds (black), males (blue) and females (red) over all nests in each 5 minute period since the nest disturbance event up to 60 minutes (n = 36 females, n = 35 males, but from 37 different nests as one nest only had a male parent and two only had female parents). The bars display the 95% confidence intervals.

Table 1. An NLS model of the change in square rooted provisioning rate per five minute block, with time since a nest disturbance event. Nest was a random effect, there were 37 groups with a total of 444 observations. The model log likelihood = -304.1, deviance = 608, residual df = 439, the standard deviation of the random asymptote for each territory is 0.298. The model equation: square rooted number of feeds in 5 minutes = 1.06/(1+exp((8.12-time since nest disturbance)/3.45)).

	Parameters estimates
Asymptote	1.06 +/- 0.004
Midpoint	8.12 +/- 0.004
Slope	3.45 +/- 0.004

Table 2. Model selection for a GAMM looking at the variation in response to nest disturbance through provisioning rate, due to differences of parental sex or in average nestling condition at 6 days old. Brood size was included in all models to control for any effect of variation in brood size between nests (3 nests of 3, 7 nests of 4, 8 nests of 5 and 19 nests of 6) on the provisioning rate. Nest was included as a random effect to account for repeated measures of provisioning rate, which was calculated for 12 five minute periods for each nest. Time = time since nest disturbance by the researcher, condition = average nestling condition for a nest when the nestlings were 6 days old, S = a smoother term, sex = male or female parent, : = interaction effect. N = 852 observations from 37 nests.

Model	AIC
S(time) + sex + brood size	1038
S(time) + sex + condition + brood size	1040
S(time) +sex : condition + brood size	1042
S(time) + brood.size	1042
S(time : sex) + sex : condition + brood size	1052
Time + sex + brood size	1089
Sex + brood size	1139

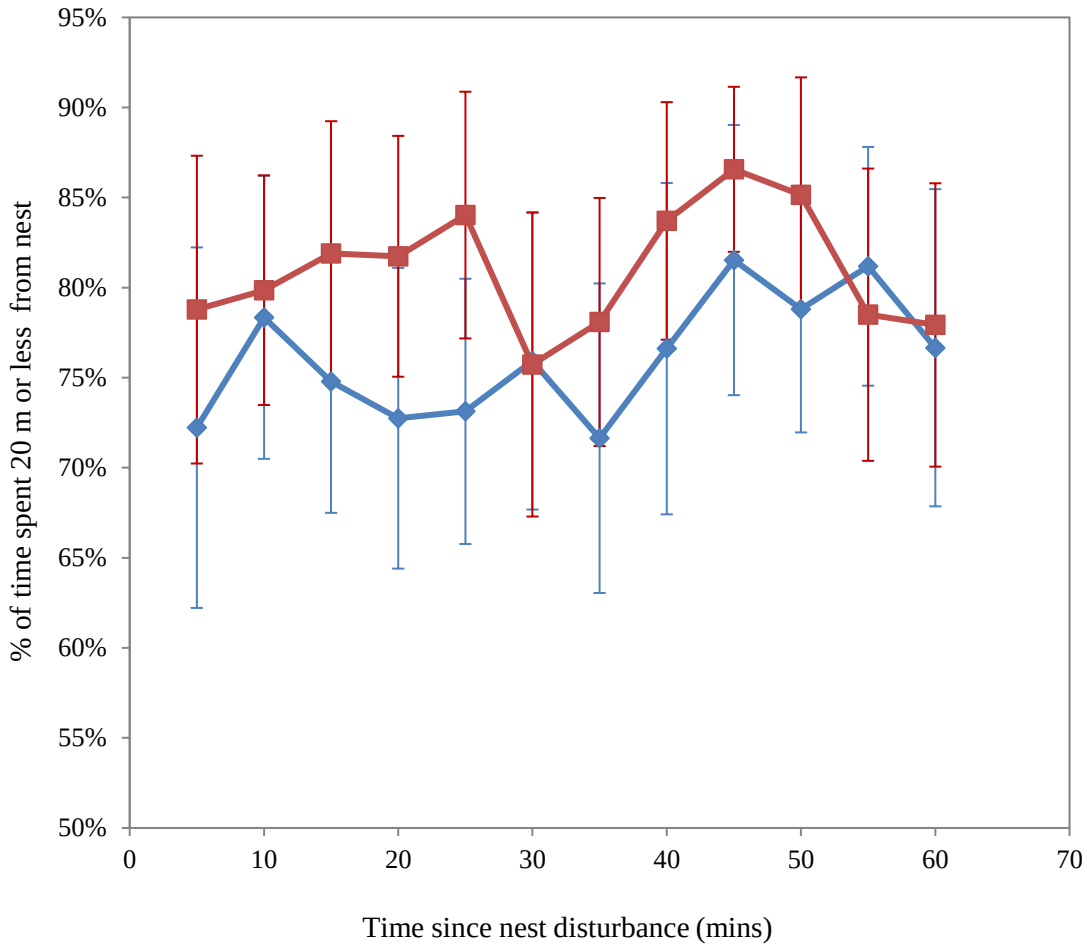
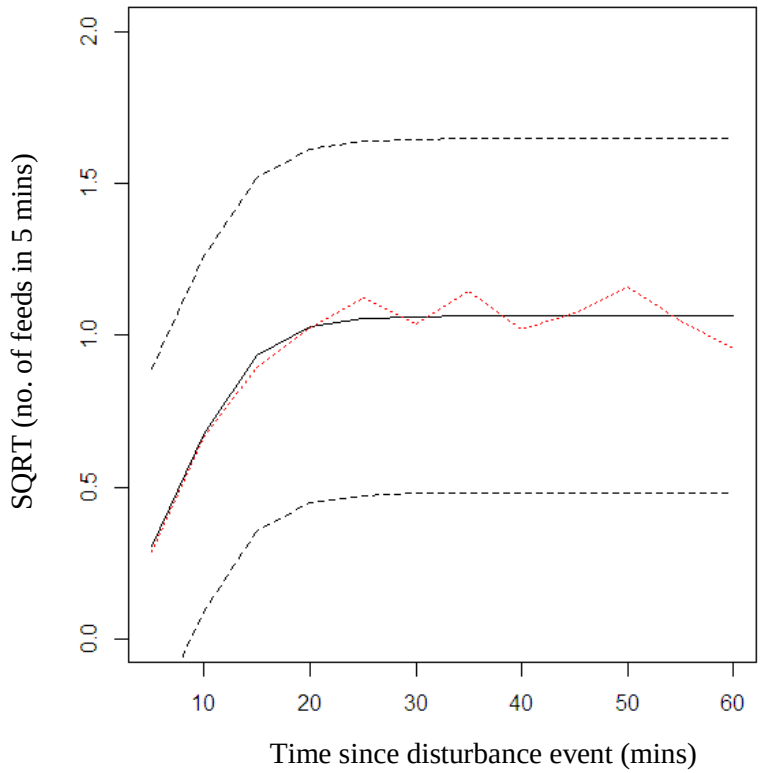


Figure 2. The mean percentage of time spent within 20 m of the nest for males (blue), and females (red), with increasing time since a nest disturbance event. The bars display the 95% confidence intervals (n = 885 observations in 39 groups).



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507 **S1.** An asymptotic random effects NLS model of the change in provisioning rate per five minute block
508 with time since a nest disturbance event, the solid line is the value for an average nest, 95% of nests are
509 within the dotted lines (n= 444 in 37 groups). The red line is the square-rooted mean provisioning rates
510 per 5 minutes block from the raw data.

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